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ASKEW, R. R.

The Biology of the British Species of the Genus *Torymus* Dalman (Hymenoptera: Torymidae) Associated with Galls of Cynipidae (Hymenoptera) on Oak, with Special Reference to Alternation of Forms

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TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 16 APRIL 1965 PART IX

The Biology of the British Species of the Genus *Torymus* Dalman (Hymenoptera : Torymidae) Associated with Galls of Cynipidae (Hymenoptera) on Oak, with Special Reference to Alternation of Forms

By R. R. Askew

(Department of Zoology, University of Manchester)

The large genus *Torymus* Dalman includes species which, as larvae, usually inhabit the galls of Cynipidae or Cecidomyidae, feeding ectoparasitically upon larvae of the gall-maker or of its parasites. Eady (1959) has revised the nomenclature of several of the European species of *Torymus* and he has been followed in naming the species associated with oak Cynipid galls. Of these, there are seven British species, *T. auratus* (Fourcroy), *T. cingulatus* Nees, *T. nigricornis* Boheman, *T. erucarum* (Schrank), *T. nobilis* Boheman, *T. amoenus* Boheman and *T. pleuralis* Thomson, and these may be divided into two biological groups. The first group, which contains *T. nigricornis, T. cingulatus* and *T. auratus,* is parasitic upon the inhabitants of galls on oak leaves. The males of these three species are very similar, especially the two former, and in order to reduce the risk of errors through misidentification the data presented below are based on females only, unless males are specifically mentioned. The second group, composed of the remaining four species, contains parasites of the inhabitants of galls growing on the roots or low down on the bole or main branches of oaks.

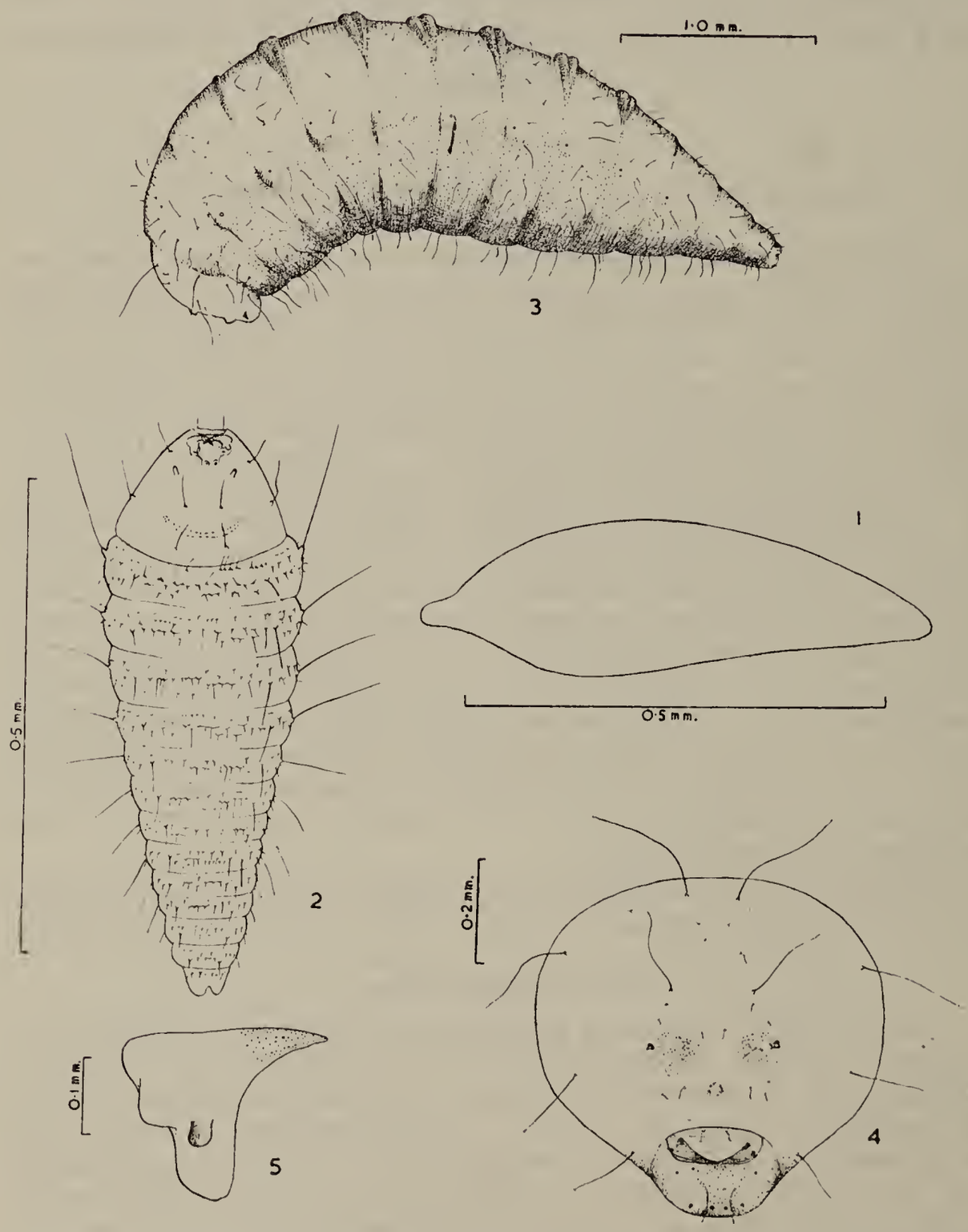
All the field observations in this study were made in Wytham Wood, Berkshire, between 1957 and 1959, unless otherwise stated.

The Immature Stages

The egg of *T. cyanimus* Boheman is described and figured by Varley (1937) and the egg of a *Torymus* species (near *phillyreae* Ruschka) by Parker (1924). Eggs of *T. bedeguaris* (Linnaeus), *T. auratus, T. cingulatus* and *T. nigricornis* (fig. 1) have been examined by the author. The eggs of all these *Torymus* species are remarkably constant in form, being cylindrical, slender, slightly curved and with a small nipple-like projection at one end. The chorion is unpigmented and unsculptured.

Torymus larvae are also very constant in form. The following account is of *T. nigricornis.* The first instar larva (fig. 2) has

thirteen body segments after the head. In dorsal view, two pairs of long setae can be seen on each body segment except the last. The most lateral setae are the longest, and on the first body segment they are directed anteriorly. In addition to these long setae, there is a transverse band of much shorter, variable, setae on all body segments. The last segment is more or less bilobed posteriorly.



Figs. 1-5.—*Torymus nigricornis* Boh. (1) Egg. (2) First instar larva. (3) Fully grown larva. (4) Head of fully grown larva in frontal view. (5) Mandible of fully grown larva.

The colour of the fully grown larva (fig. 3) varies from white to pale cream, and is imparted by the fat bodies, which are very closely packed and show through the integument. The gut also shows through the body wall as a dark area in some of the smaller individuals with less well-developed fat bodies. Of nine larvae measured, the average length was 3·3 mm., and the average depth at the fourth segment 1·3 mm. The largest specimen was 6·0 mm. long and 2·4 mm. deep. Maximum depth is attained at the fourth segment, after which the body gradually tapers towards the posterior end, more abruptly towards the head. Median dorsal protuberances are found intersegmentally between body segments two and nine. There are very slight lateral prominences on the first few spiracular segments. Long, fine setae are present on all segments, but are more numerous on the first three. They are longer ventrally. Their disposition and number are variable from segment to segment and from individual to individual, although there appears to be a tendency for certain series of setae to be repeated. There are nine pairs of spiracles, segments two to ten each bearing a pair towards their anterior borders.

The head of the fully grown larva (fig. 4) viewed from the front, is pear-shaped and the simple, pointed mandibles (fig. 5) are its most obvious structures. The small antennae are situated near to the apices of raised areas on the frons, and between them and the clypeus is a slight median elevation. There are five pairs of long setae on the frons whose arrangement (fig. 4) was constant in all individuals examined. Shorter setae are also present but their distribution varies considerably, and they are seldom symmetrically arranged about the mid-line.

Torymus auratus (Fourcroy)

The dates of emergence from galls and of field captures have shown *T. auratus* to have two generations during a year. Females of the first generation were captured in Wytham Wood from the third quarter of April to the second quarter of July, and females of the second generation throughout September and October and well into November (fig. 6). Second generation insects were taken more frequently than those of the first generation.

The first generation of *T. auratus* emerges from the spangle galls of *Neuroterus albipes* f. *laeviusculus* Schenck, *N. quercus-baccarum* f. *lenticularis* (Olivier) and *N. numismalis* (Geoffroy) in spring. Insects of this generation were observed drilling with their ovipositors into new galls of *Andricus curvator* Hartig, *Neuroterus tricolor* (Hartig), *Biorhiza pallida* (Olivier), *Cynips longiventris* Hartig and *C. divisa* Hartig, and in addition its immature stages were found in galls of *Cynips disticha* Hartig (Rosthwaite, Cumberland). In autumn, insects of the second generation emerged from galls of *Andricus curvator, A. quercus-ramuli* (Linnaeus), *A. scminationis* (Giraud), *A. quadrilineatus* Hartig, *A. inflator* Hartig, *Neuroterus albipes* (Schenck), *N. tricolor, N. numismalis* f. *vesicator* (Schlechtendal), *N. quercus-*

baccarum (Linnaeus) and *Biorhiza pallida*. Insects of this second generation were observed attacking all of the three spangle galls in which the species overwinters as a fully-grown larva. Numbers of reared females are included in table 1.

Usually only one egg is laid on a host, which is paralysed, but in one gall of *N. quercusbaccarum* twelve eggs were found on a prepupa of the gall maker; possibly the product of more than one female.

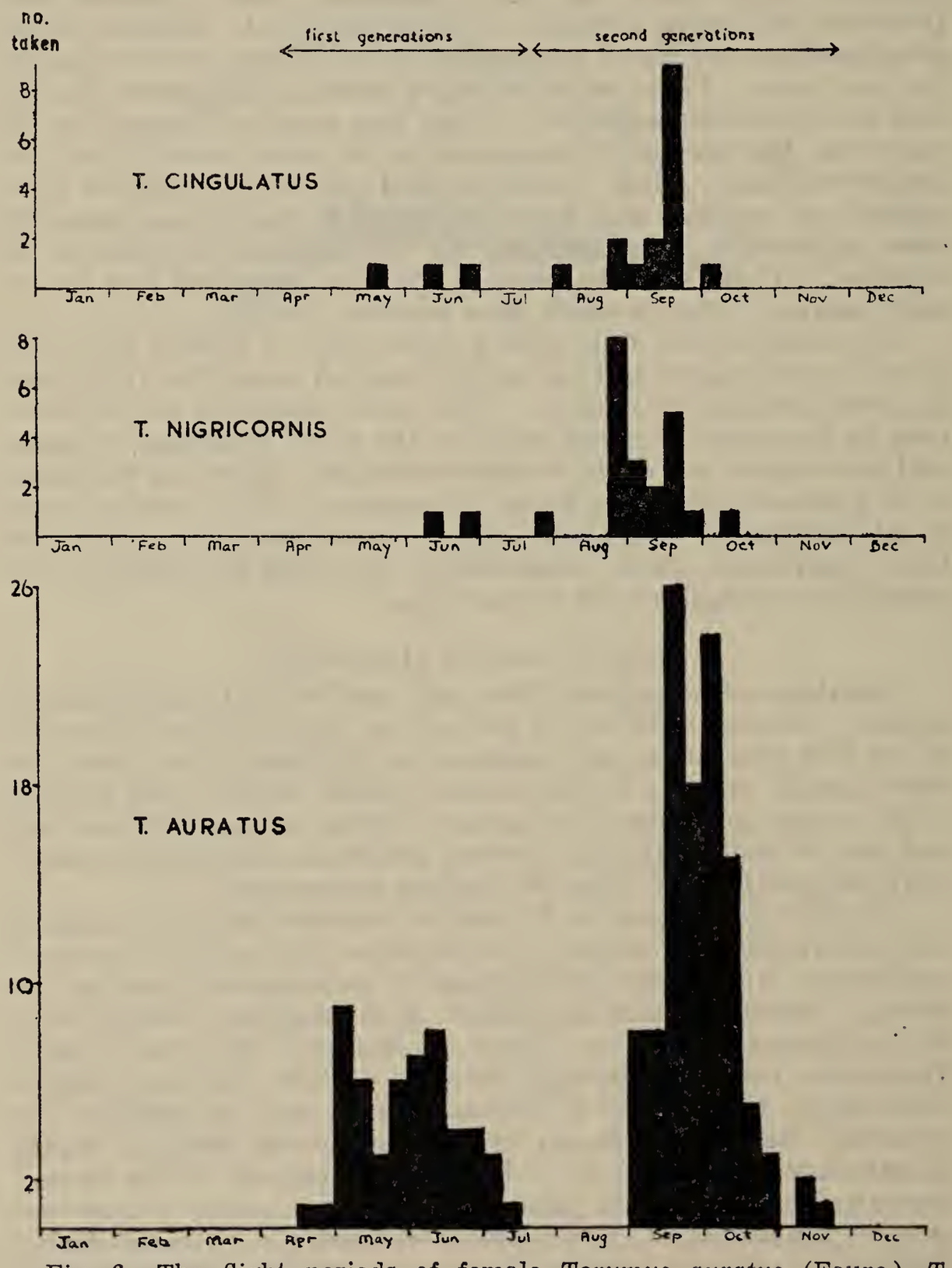


Fig. 6.—The flight periods of female *Torymus auratus* (Fourc.), *T. cingulatus* Nees and *T. nigricornis* Boh. in Wytham Wood.

TABLE 1

Numbers of reared female *Torymus auratus*, *T. cingulatus* and *T. nigricornis* examined.

Host Galls	*T. cingulatus* Gen. I	*T. cingulatus* Gen. II	*T. nigricornis* Gen. I	*T. nigricornis* Gen. II	*T. auratus* Gen. I	*T. auratus* Gen. II
C. divisa	29	—	11	—	—	—
C. longiventris	8	—	3	—	—	—
C. quercusfolii	—	—	42	—	—	—
B. pallida	8	41	1	51	—	90
N. quercusbaccarum	—	—	—	—	—	12
N. tricolor	—	—	—	—	—	1
N. n. f. vesicator	—	—	—	—	—	1
N. albipes	—	—	—	—	—	1
N. q.-b. f. lenticularis	—	—	—	—	20	—
N. a. f. laeviusculus	—	—	—	—	6	—
N. numismalis	—	—	—	—	6	—
A. fecundator	—	—	1	—	—	—
A. kollari	24	—	74	—	—	—
A. curvator	—	—	—	—	—	11
A. inflator	—	—	—	—	—	2
A. quercusramuli	—	—	—	—	—	3
A. seminationis	—	—	—	—	—	1
A. quadrilineatus	—	—	—	—	—	1

The table includes specimens from the following localities in addition to Wytham Wood:

T. cingulatus
- ex *B. pallida* galls, Arbrook Common, Surrey; Isle of Wight; Borrowdale, Cumberland.
- ex *C. divisa* galls, Cothill, Berkshire; Rugby, Warwickshire.
- ex *A. kollari* galls, Cothill, Berkshire; Orpington, Kent.

T. nigricornis
- ex *B. pallida* galls, Isle of Wight.
- ex *C. quercusfolii* galls, Borrowdale, Cumberland; Hell Coppice, Buckinghamshire.
- ex *A. kollari* galls, Malvern, Worcestershire; Gosforth, Northumberland; Orpington, Kent; Enfield, Middlesex; Etrop Green, Cheshire.
- ex *A. fecundator* galls, Ernocroft Wood, Cheshire.

T. auratus
- ex *N. numismalis* galls, Cathiron, Warwickshire; Cothill, Berkshire; Hell Coppice, Buckinghamshire.
- ex *N. quercusbaccarum* galls, Fencehouses, Durham.
- ex *B. pallida* galls, Cathiron, Warwickshire; Borrowdale, Cumberland; Oxshott, Surrey; Isle of Wight; Cothill, Berkshire.
- ex *N. q.-b. f. lenticularis* galls, Ernocroft Wood, Cheshire.

T. auratus was found attacking *Synergus gallaepomiformis* (Fonscolombe) and *S. albipes* Hartig larvae in galls of *N. quercusbaccarum*. In galls containing several *Synergus* in separate cells, each *Synergus* may be parasitised, but more than one adult *T. auratus* was never reared from a single gall of *N. quercusbaccarum*. As the *Torymus* larvae grow, they chew through the thin membranes separating the *Synergus* cells, and apparently only one is able to survive. Leaf and catkin galls of *N. quercusbaccarum* are about equally attacked by *T. auratus*.

T. auratus was not reared from galls of the agamic generations of *Cynips*, but in July a few galls of *C. divisa* and *C. longiventris*

were found to contain eggs or first instar larvae of *T. auratus* on the gall making larvae. Failure to rear adult *T. auratus* from these *Cynips* galls is probably due to their destruction by later parasites (Askew, 1961).

Other species of Cynipidae or their parasites attacked by *T. auratus* were *Pediobius lysis* (Walker) (*N. numismalis* gall), *Mesopolobus tibialis* (Westwood) (*N. tricolor* galls), *Mesopolobus* sp. (*A. curvator* gall), *Eurytoma brunniventris* Ratzeburg (*A. curvator* gall), *Olynx arsames* (Walker) (*A. curvator* galls), *Syntomaspis notata* (Walker) (*A. curvator* galls), *Synergus gallaepomiformis* (*A. curvator* galls), *Synergus nervosus* Hartig (*A. curvator* gall), *N. quercusbaccarum, N. quercusbaccarum* f. *lenticularis, N. numismalis, N. tricolor, A. quadrilineatus, A. seminationis, A. curvator* and *A. inflator.*

There are differences of colour and form between individuals of the two generations of *T. auratus.* Insects of the first generation are darker and more bronzed than second generation insects, and typically all the femora and the hind tibiae are marked with metallic green. Second generation insects are a very much brighter green, with generally only the hind femora marked with metallic green.

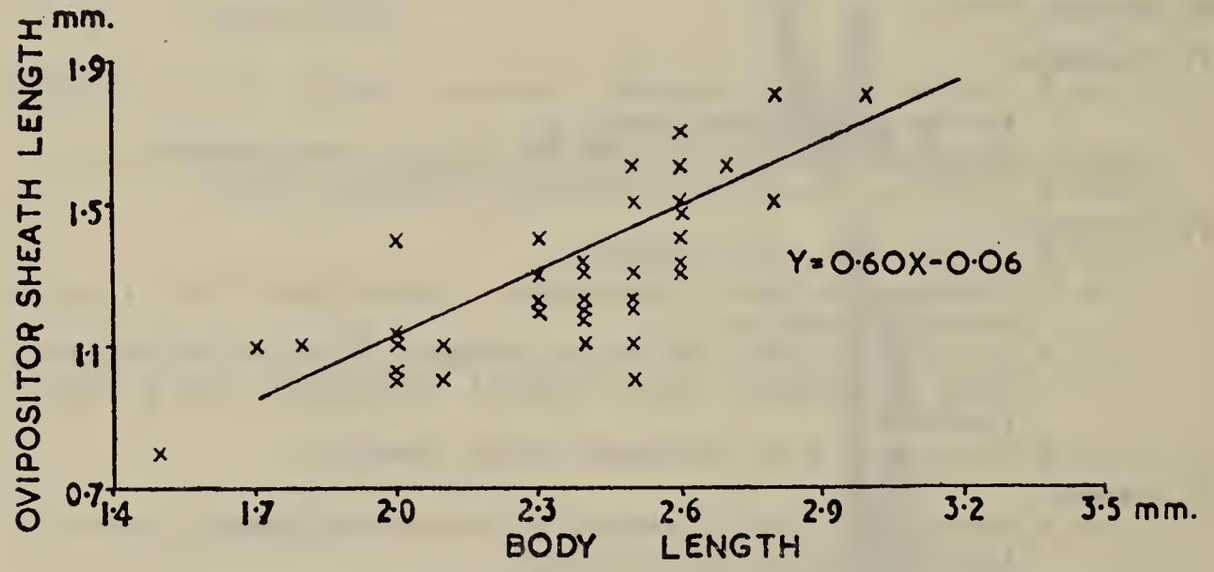


Fig. 7.—The relationship between ovipositor sheath length and body length in the second generation of *Torymus auratus* (Fourc.). This generation is described as having short ovipositors. The measurements were made on dry specimens. 'Body length' is the distance from the frons to the base of the ovipositor sheaths. Differential shrinkage of the gaster after death could be ignored since the length of the gaster was found to vary directly with the length of the thorax plus propodeum.

There is a very marked difference in relative lengths of the ovipositor sheaths (third valves) between second and most first generation insects. Insects of the second or autumn generation always have short ovipositor sheaths (fig. 7), whilst those of the first or spring generation are dimorphic, sometimes having short ovipositor sheaths of the same length as those of second generation insects, but most often having considerably longer ovipositor

sheaths (fig. 8). The difference between long and short sheathed *T. auratus* is so marked that they were regarded as separate species until Eady (1959 and pers. comm.) showed them to be forms of the same species by rearing short sheathed individuals from galls attacked by long sheathed individuals.

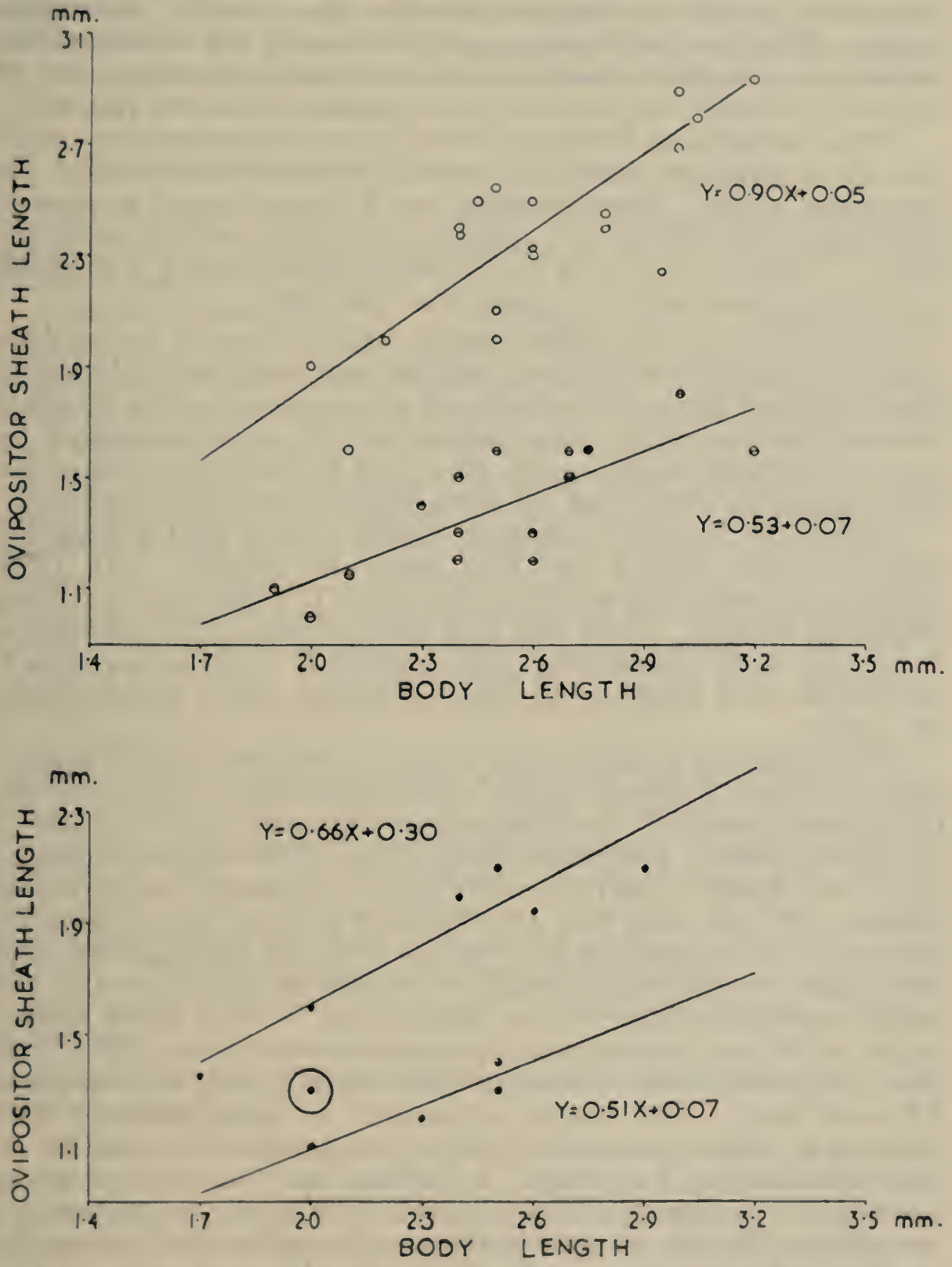


Fig. 8.—The relationship between ovipositor sheath length and body length in the first generation of *Torymus auratus* (Fourc.), which is dimorphic. *Above*: field caught specimens. o=long sheathed forms; θ=short sheathed forms. *Below*: adults of the first generation resulting from larvae 'forced' during winter indoors. The ringed point was ignored in calculating the fit of the line.

Adult *T. auratus* of the first generation, 'forced' out in the winter from galls collected in the autumn by keeping in a warm room, always resemble in colour insects of the second generation. Their ovipositor sheaths however are of two lengths, as in naturally reared first generation insects. The form with short ovipositor sheaths is indistinguishable from second generation insects. The form with long ovipositor sheaths has sheaths intermediate in length between those of second generation and of naturally reared, long sheathed, first generation insects. (fig. 8).

Colour differences between insects of the two generations would seem to be induced entirely by some climatic factor acting on the immature stages. Overwintering as a larva causes a general darkening and increase in quantity of metallic coloration in the adult. This does not occur with insects overwintering in a warm, dry room, either inside or outside the host gall.

With regard to ovipositor sheath length, there is evidently a genetic rhythm between short sheathed and a mixture of long and short sheathed forms. The degree of expression of a long sheath is however influenced by some climatic factor, as demonstrated by the intermediate sheath length displayed by 'forced' adults of the first generation which had not been exposed to winter conditions.

Among 21 female *T. auratus* caught in the field during the spring of 1958, only 9 had long ovipositor sheaths. In 1959, however, among 23 female first generation *T. auratus,* 19 had long ovipositor sheaths. Both long and short sheathed first generation *T. auratus* were reared from collections of *N. quercusbaccarum* f. *lenticularis* galls kept in identical conditions out of doors during the winter.

The ovipositor sheath length varies directly with the ovipositor (first and second valves) length, and the ovipositor lengths in the two generations of *T. auratus* can be correlated with the size of the galls attacked. The mean sheath length of 38 second generation insects was found to be 1·28 ± 0·04 mm. An insect with ovipositor sheaths 1·28 mm. long had an ovipositor 2·1 mm. long, measured from apex to junction of first valves with the gonangulum, and this would be just long enough to penetrate to all parts of the larval chamber of the largest spangle gall. The mean sheath length of 19 long sheathed first generation insects was 2·36 ± 0·08 mm. An insect with average sheath length had an ovipositor 3·9 mm. long. The longer ovipositors in long sheathed first generation insects enables the large spring galls of *B. pallida, N. quercusbaccarum, N. tricolor, A. inflator* and *A. curvator* to be attacked. The first generation insects with short ovipositors are probably only able to attack the smaller galls of *C. divisa, N. numismalis* f. *vesicator* and *N. albipes* (fig. 11).

With regard to the number of different types of oak galls attacked, *T. auratus* is second only to *Eurytoma brunniventris* Ratzeburg (Askew, 1961) among the chalcid inhabitants of oak galls, attacking at least fifteen different types. The first generation attacks leaf galls (e.g. *N. tricolor*), bud galls (e.g. *B. pallida*)

and catkin galls (e.g. *A. quadrilineatus*). Only root galls and galls on the trunk appear to be immune from attack. The second generation is entirely confined to spangle galls. The leaf galls of *A. ostreus* (Hartig) would seem to be suitable for attack, being of approximately the same size as spangle galls beside which they often grow. However this association has not yet been discovered. The large host gall range of the first generation is rendered possible by the range of ovipositor length, and by the polyphagous nature of the larvae (*vide* above).

Torymus cingulatus Nees and *T. nigricornis* Boheman

Like *T. auratus*, these two species go through two generations during a year. Corresponding generations of all three species are almost synchronous (fig. 6).

The first generations of *T. cingulatus* and *T. nigricornis* are small in numbers and are in flight in May and June. The second generations are much more numerous and are in flight principally at the end of August and in September, but specimens have also been taken in October and (*T. nigricornis*) at the end of July.

First or spring generation insects of both species have been reared from galls of *C. divisa, C. longiventris, B. pallida* and *Andricus kollari* Hartig, in which they overwinter as fully grown larvae. In addition, *T. nigricornis* has emerged from galls of *Cynips quercusfolii* Linnaeus and *Andricus fecundator* (Hartig) in spring. The galls of *B. pallida* were still attached to the tree when collected in winter. What appeared to be males of *T. cingulatus* emerged from a few galls of *A. ostreus* in spring.

A female *T. nigricornis* of the first generation was observed drilling with its ovipositor into a new gall of *B. pallida* in the second week of June. Galls of *B. pallida*, gathered in July, yielded specimens of the second generation of both *T. cingulatus* and *T. nigricornis*. Two male *T. nigricornis* (?) also emerged from first-year galls of *N. quercusbaccarum*. Insects of these second generations attack the galls in which the species overwinters (*vide* above). *T. nigricornis* was observed attacking galls of *A. kollari, C. divisa* and *C. longiventris*, and *T. cingulatus* galls of *C. divisa*, in autumn.

Total numbers of females of both species reared from galls are given in table 1.

There are differences in colour between individuals of the two generations, as in *T. auratus*. In *T. nigricornis*, insects of the first generation tend to be more bronzed on the head and thorax than second generation insects, and their legs are usually darker in colour, with larger areas of metallic coloration on the femora, particularly on the hind femora. Similar colour differences are found in the two generations of *T. cingulatus*, but they are seldom so pronounced as in *T. nigricornis*. The testaceous band at the base of the female gaster of *T. cingulatus* is usually larger and brighter in specimens of the second generation.

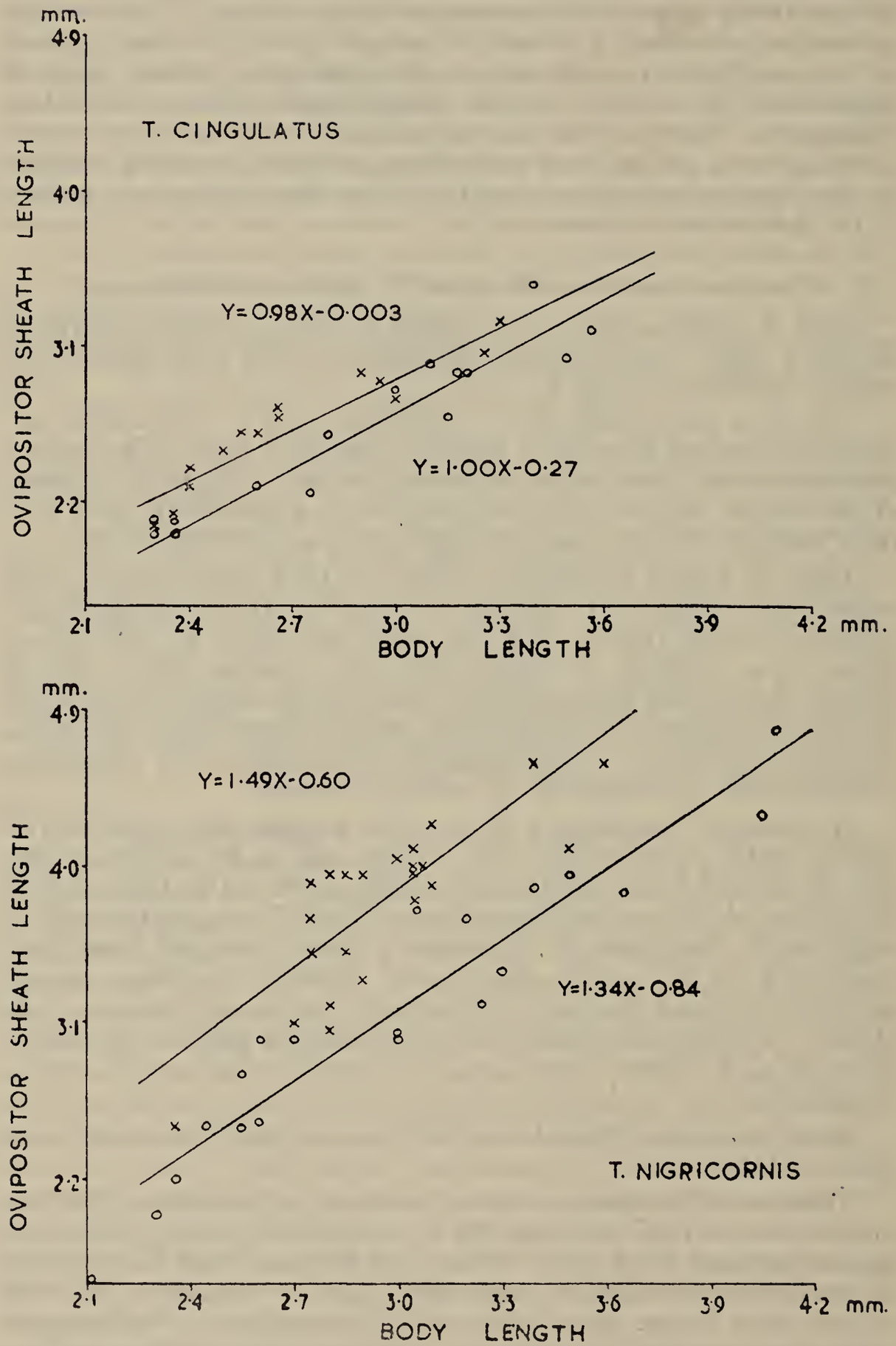


Fig. 9.—The relationship between ovipositor sheath length and body length in *Torymus cingulatus* Nees (above) and *T. nigricornis* Boh. (below), caught in the field. o=first (spring) generations. x=second (autumn) generations.

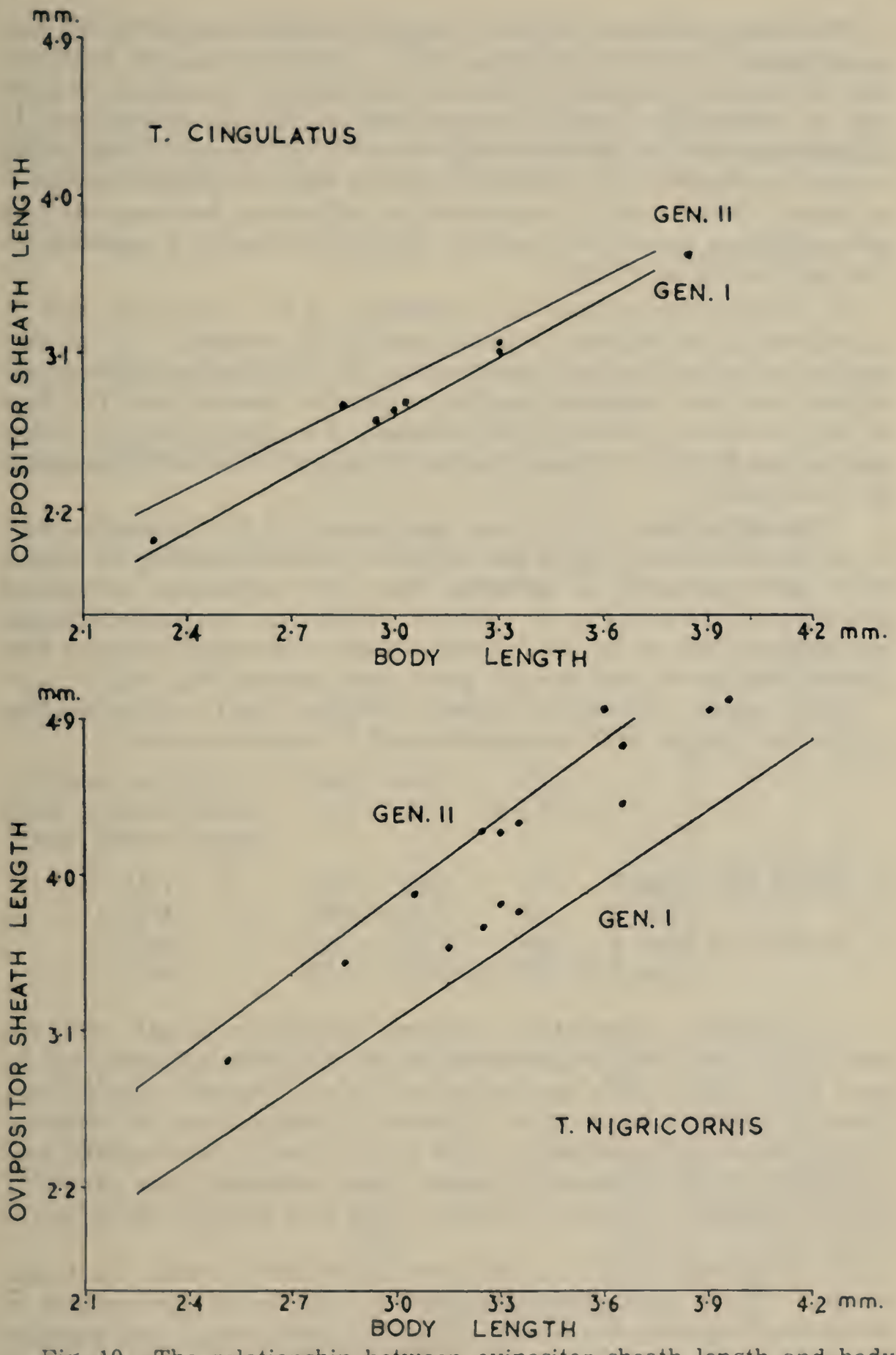


Fig. 10.—The relationship between ovipositor sheath length and body length in 'forced' *Torymus cingulatus* Nees (above) and *T. nigricornis* Boh. (below) of the first (spring) generations. The lines represent the naturally occurring condition (fig. 9) in these two species; the points represent the condition of 'forced' insects, which have ovipositor sheaths approaching in length those of field caught second generation insects.

The length of the ovipositor sheaths is also different in the two generations. In *T. nigricornis,* first generation insects have relatively shorter ovipositor sheaths than second generation insects (fig. 9), with only a small overlap between the two generations; a significance test on the difference between the means of the ratios ovipositor sheath length/body length in the two generations gave a value $P<0{\cdot}01$. In *T. cingulatus* the difference between the two generations is much less marked (fig. 9), but again a significance test gave a value $P<0{\cdot}01$.

It is interesting that the condition in *T. cingulatus* and *T. nigricornis* is the reverse of that found in *T. auratus.* In the two species at present under consideration, it is the second generations which have the relatively longer ovipositor sheaths, not the first as in *T. auratus.* There is no evidence of a dimorphism in either generation of either species, such as is found in the first generation of *T. auratus.*

'Forced' adults of the first generation of *T. cingulatus* and *T. nigricornis,* emerging in the warmth of the laboratory in winter from galls gathered in autumn, have the coloration of second generation insects, as in *T. auratus.* Also, the ovipositor sheaths are intermediate in length between those of naturally reared first generation insects and second generation insects (fig. 10).

The mean ovipositor sheath lengths and corresponding ovipositor lengths of *T. cingulatus* and *T. nigricornis* are:

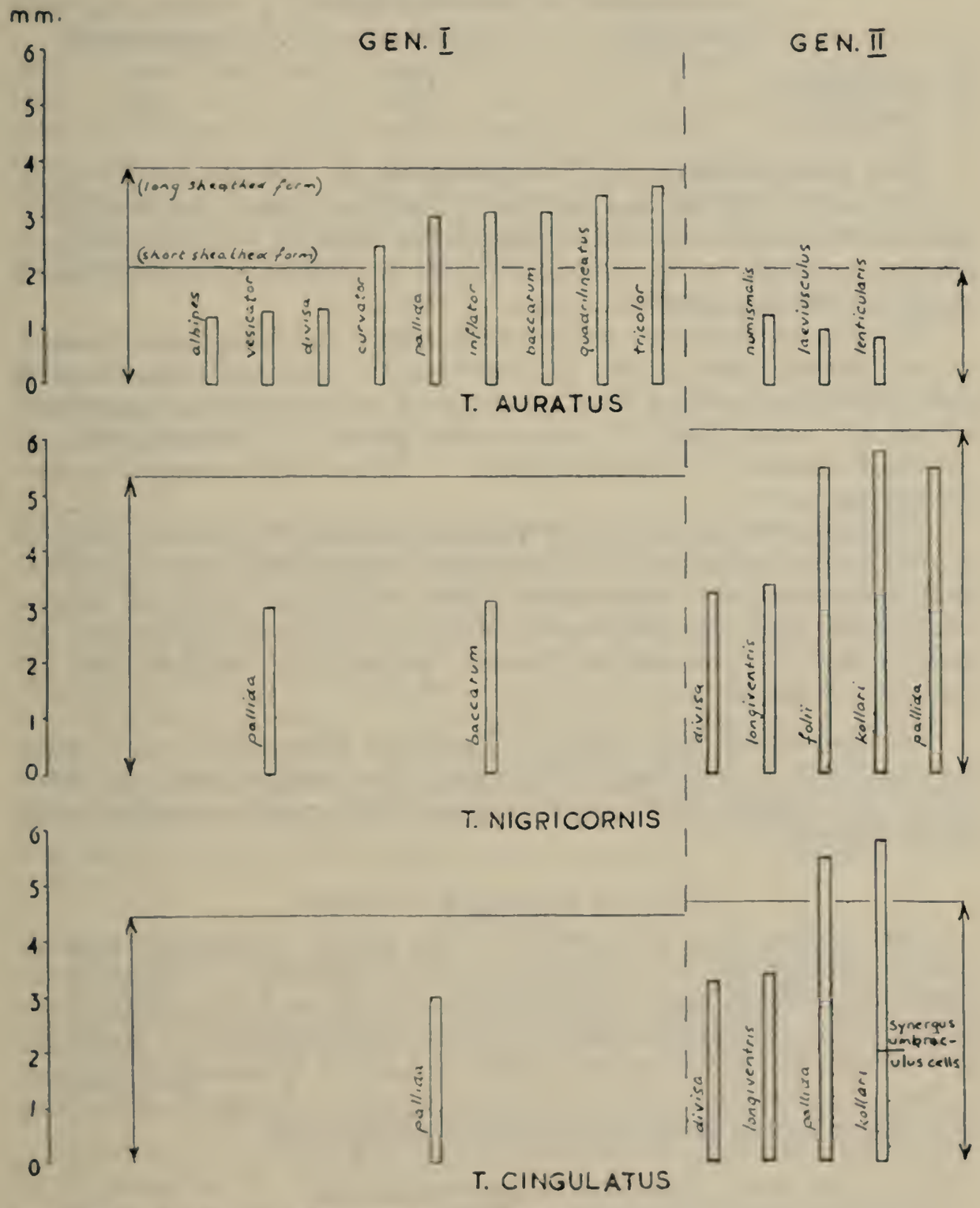
		No. examined	Mean sheath length (mm.)	Ovipositor length corresponding to mean sheath length (mm.)
T. cingulatus	Gen. I	15	2·64 ± 0·05	4·45
,,	Gen. II	14	2·65 ± 0·08	4·70
T. nigricornis	Gen. I	20	3·16 ± 0·17	5·35
,,	Gen. II	23	3·78 ± 0·10	6·15

The positive correlation between ovipositor length and the size of the host galls is illustrated in fig. 11, from which it will be seen that larger galls are attacked by the second generations. Long ovipositors are brittle. Broken off ovipositors of *Torymus* have been found penetrating galls of *C. divisa, C. quercusfolii* and *A. kollari,* and ovipositors longer than necessary are probably selected against. Long ovipositors may also present problems in flight.

T. cingulatus and *T. nigricornis* have very similar host gall ranges. Their ecological separation in the second generation in which both species develop in *B. pallida* galls may be effected by *T. nigricornis* attacking larvae deeper in the gall than *T. cingulatus,* which latter has the shorter ovipositor.

In the first generation, *T. nigricornis* is a common parasite of the large leaf gall of *C. quercusfolii,* but *T. cingulatus* does not appear to attack this gall. The reason is unknown. Instead it is frequently found attacking the smaller leaf galls of *C. divisa* and

C. longiventris. These latter two galls are only occasionally attacked by *T. nigricornis*. Both species frequently attack the large bud galls of *A. kollari* but the different ovipositor lengths in the two *Torymus* species ensure a qualitative difference in the hosts attacked. The gall of *A. kollari* is attacked by two common inquiline Cynipids, *Synergus umbraculus* (Olivier) and *S. rein-*



ARROWS represent mean ovipositor length.
RECTANGLES represent mean distance (20 galls) from exterior of gall to farthest point of larval chamber at time of attack.

Fig. 11.—Diagram to illustrate the correlation between ovipositor lengths in the two generations of *Torymus auratus* (Fourc.), *T. cingulatus* Nees and *T. nigricornis* Boh. and the sizes of the galls attacked.

hardi Mayr. *S. umbraculus* larvae live in cells towards the periphery of the gall, while cells containing the larvae of *S. reinhardi* are found in the centre of the gall in place of the central cell of the gall maker. The distribution of *T. cingulatus* and *T. nigricornis* in galls of *A. kollari,* as ascertained by rearing adults from the larvae found in the different cells, is as follows:

	A. kollari cells (central)	*S. reinhardi* cells (central)	*S. umbraculus* cells (peripheral)
T. nigricornis	4	15	1
T. cingulatus	—	4	4

The predominance of *T. nigricornis* in the main cell of *A. kollari* and in the central cells of *S. reinhardi,* and the predominance of *T. cingulatus* in the peripheral cells of *S. umbraculus* is almost certainly to be correlated with the difference in ovipositor length in the two species.

T. cingulatus larvae were found attacking *Eurytoma brunniventris* larvae and pupae (*A. ostreus, C. divisa, C. longiventris* galls), *Synergus albipes* Hartig larvae (*A. ostreus* galls), *S. nervosus* larvae (*C. divisa* gall), *S. umbraculus* larvae (*A. kollari* galls), *S. reinhardi* larvae (*A. kollari* galls), *C. divisa* larvae and *C. longiventris* pupae.

T. nigricornis larvae were found attacking *Eurytoma brunniventris* larvae (*C. divisa, C. quercusfolii* galls), *Eudecatoma biguttata* (Swederus) (*C. quercusfolii* galls), *Synergus reinhardi* larvae (*A. kollari* galls), *S. pallicornis* Hartig (*C. quercusfolii* galls), *A. kollari* and *C. quercusfolii* larvae, pupae and adults, and *A. fecundator* larvae.

The remaining four species of *Torymus,* considered below, were not common in Wytham Wood, and the meagre data on them from that locality have been implemented where possible from other sources.

Torymus erucarum (Schrank)

This species may be specific to the gall of *Andricus quercusradicis* (Fabricius) in which it is fairly common. Thirty-four female and fifteen male specimens have been seen from galls from Surrey, Kent, Berkshire, Isle of Wight and Lancashire. Remains of *T. erucarum* were found in cells of both *A. quercusradicis* and of the inquiline *Synergus incrassatus* Hartig. Adult *T. erucarum* were taken in the field in July and in September.

Torymus nobilis Boheman

Reared specimens of this species seen by the author are three females from galls of *Biorhiza pallida* f. *aptera* (Fabricius) (Hope Dept., Oxford), a number from galls of *Andricus testaceipes* f. *sieboldi* (Hartig) collected in the New Forest by C. R. Vardy (British Museum (Nat. Hist.)), and six females and two males from galls of *Andricus quercusradicis* (Isle of Wight, M. J. Cotton).

Connold (1908) also records the species as a parasite in the gall of *B. pallida* f. *aptera*.

Torymus amoenus Boheman

Apparently rare, I have no rearing records for this species. A single female was taken on oak in Wytham Wood on 25th June 1958. Connold (1908) records it as a parasite of *Trigonaspis megaptera* (Panzer).

Torymus pleuralis Thomson

This species appears to be most frequently associated with the gall of *Andricus quercusradicis* from which fifteen females and three males have been reared from Berkshire and Surrey. In addition, there are four male *Torymus*, probably attributable to this species, in the Manchester Museum, reared from galls of *Trigonaspis megaptera* (Westmorland, H. Britten).

Hoffmeyer (1931) lists the host galls of these four latter species of *Torymus* in Denmark as follows:

	T. nobilis	*T. erucarum*	*T. amoenus*	*T. pleuralis*
A. quercuscorticis	×	–	×	×
A. quercuradicis	×	×	×	×
A. rhizomae	×	–	×	–
A. t. f. *sieboldi*	×	–	×	–
T. megaptera	×	–	–	–

In addition I have seen specimens of *T. pleuralis* from *A. testaceipes* f. *sieboldi* galls from La Rochelle, France (R. Folliot).

All the galls recorded as hosts of these four species of *Torymus* have one striking feature in common. Although very different in form, they all grow either on the oak roots (*B. pallida* f. *aptera*, *A. quercusradicis*) or low down on the oak bole or main branches (*A. rhizomae* (Hartig), *A. quercuscorticis* (Linnaeus), *A. quercusradicis*, *A. testaceipes* f. *sieboldi*, *T. megaptera*).

Too little information is at present available to show how these *Torymus* are ecologically separated, but it seems that they never attack the same types of galls as *T. auratus*, *T. cingulatus* or *T. nigricornis*.

Summary

1. The immature stages of *Torymus* are described, and the biologies of *T. auratus* (Fourcroy), *T. cingulatus* Nees, *T. nigricornis* Boheman, *T. erucarum* (Schrank), *T. nobilis* Boheman, *T. amoenus* Boheman and *T. pleuralis* Thomson are discussed.
2. All the species are polyphagous ectoparasites of gall-forming Cynipidae on oak, or of their inquilines or chalcidoid parasites.
3. *T. auratus*, *T. cingulatus* and *T. nigricornis* have two generations during a year. The overwintering generation of *T. auratus* is parasitic in spangle galls of *Neuroterus*, while the autumn generation is parasitic in a variety of galls of the genera *Cynips*, *Neuroterus*, *Andricus* and *Biorhiza* growing on oak leaves, catkins or buds. The overwintering generations of *T. cingulatus* and *T. nigricornis* emerge in spring from galls of *Cynips*, *Andricus* and *Biorhiza* on leaves and buds, while the autumn generations of these two species are usually parasitic in the gall of *Biorhiza pallida* (Olivier).

4. The females of *T. auratus, T. cingulatus* and *T. nigricornis* have ovipositors of different lengths, and further, the length of the ovipositor is different in the two generations of the same species. The difference between the two generations is most marked in *T. auratus* in which insects of the first or overwintering generation usually have much longer ovipositors than those of the second generation. However some first generation insects have short ovipositors. In *T. cingulatus* and *T. nigricornis,* insects of the first generation have shorter ovipositors than those of the second generation. There are also colour differences between the two generations in these three species.
5. When insects of the first generation are overwintered indoors they resemble in colour second generation insects, but their ovipositor length is intermediate between that of naturally reared first and second generation insects. It is concluded that climatic factors are responsible for differences in colour between the two generations, but that the ovipositor length is controlled by genetic factors whose expression is modified by climatic factors.
6. The length of the ovipositor in the different generations of these three *Torymus* species may be correlated with the size of the galls attacked, and sometimes with the position of different hosts in galls containing several larval chambers. In this way interspecific competition is minimised.
7. *T. erucarum, T. nobilis, T. amoenus* and *T. pleuralis* all attack galls growing either on the oak roots or low down on the oak bole or main branches. They never attack the same types of galls as *T. auratus, T. cingulatus* or *T. nigricornis.*

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